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THE TAXONOMIC POSITION OF *BENTHARCA XENOPHORICOLA* (KURODA, 1929) AND *BENTHARCA RUBROTINCTA* KURODA & HABE IN HABE, 1958 (BIVALVIA: ARCIDAE)

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ABSTRACT

Bentharca xenophoricola (Kuroda, 1929) and *Bentharca rubrotincta* Kuroda & Habe in Habe, 1958, from Japan are re-examined. Based on comparison with the material of *Bentharca asperula* (Dall, 1881) and *Asperarca nodulosa* (Müller, 1776), the type species of *Bentharca* Verrill & Bush, 1898, and *Asperarca* Sacco, 1898, respectively, as well as on the description, pictures, and photos of *Deltaodon tugelae* Barnard, 1962, the type species of *Deltaodon* Barnard, 1962, the following new combinations are suggested: *Asperarca xenophoricola* (Kuroda, 1930) and *Deltaodon rubrotincta* (Kuroda & Habe in Habe, 1958). *Asperarca xenophoricola* has an elongate, inflated, thick shell, with a weakly hirsute periostracum, commarginal lamellate ridges made nodulose by the closely spaced, high radial riblets, and narrow, slightly curved hinge plate, with teeth divided into anterior and posterior sets by a narrow edentulous gap. The anterior set of this species has 7–14 long teeth; the posterior set 6–9 oblique teeth that diverge to a varying degree. This species occurs off Japan, China, and southeastern Australia at depths from 50 to 500 m. *Deltaodon rubrotincta* has a high, moderately inflated, thick, reddish-brown shell, with white rays and spots, commarginal lamellate ridges and high, nodules, widely spaced radial ribs, a broad, strongly curved hinge plate, with teeth divided into anterior and posterior sets by a shallow, oblique groove. The anterior set of this species forms an oval group of 4–7 long, mostly curved, boomerang-shaped teeth. The posterior set has 9–18 long, oblique teeth that diverge to a varying degree. This species occurs off Japan and China at depths from 100 to 200 m. Expanded descriptions of these species are presented.

Key words: *Bentharca*, *Asperarca, Deltaodon,* systematics, morphology, distribution, northwestern Pacific.

INTRODUCTION

Bentharca Verrill & Bush, 1898, species are widely distributed in the world's oceans (Dall, 1881; Verrill & Bush, 1898; Knudsen, 1967, 1970; Oliver & Allen, 1980; Oliver & Cosel, 1993), including the North Pacific (Kuroda, 1930; Habe, 1958, 1977, 1981; Li, 1984; Habe et al., 1986; Hayami & Kase, 1993; Higo et al., 1999; Coan et al., 2000; Okutani, 2000). The shell morphology of most species of *Bentharca* has been described in detail (Dall, 1881; Knudsen, 1967, 1970; Oliver & Allen, 1980; Hayami & Kase, 1993; Coan et al., 2000). Exceptions are *Bentharca xenophoricola* (Kuroda, 1929) and *Bentharca rubrotincta* Kuroda & Habe in Habe, 1958. The descriptions of these species given in the literature are brief (especially for *B. xenophoricola*) and sometimes without illustrations (Kuroda, 1929, 1930; Habe, 1951, 1958, 1977; Li, 1984; Okutani, 2000). The present study of the shell morphology of these species and the representatives of other genera of the Arcidae has shown that *B. xenophoricola* and *B. rubrotincta* should be placed in the genera *Asperarca* Sacco, 1898, and *Deltaodon* Barnard, 1962, respectively. In this paper, I give expanded descriptions of *B. xenophoricola* and *B. rubrotincta*, supplemented by new data on their shell morphology that support the new combinations.

MATERIAL AND METHODS

Material Studied

The collections of the following taxa were used: *Bentharca asperula* (Dall, 1881) (LACM, MIMB, NMNZ, NMW, NSMT); *Asperarca nodulosa* (Müller, 1776) (NMW); *B. rubrotincta* (NSMT); *B. xenophoricola* (NMW); *Samacar strabo* (Hedley, 1915) (AMS); *Samacar pacifica* (Nomura & Zinbo, 1934) (NSMT, SBMNH); several species of *Acar* Gray, 1857; *Barbarca* Dall, Bartsch & Rehder, 1938; *Barbatia* Gray, 1842; *Bathyarca* Kobelt, 1891; *Coraliarca* Habe & Okutani, 1968; *Hawaiarca* Dall, Bartsch & Rehder, 1938; and *Mimarcaria* Iredale, 1939 (CAS, MIMB, NSMT, RBCM, SBMNH, UW, ZIN). *Bentharca asperula* from New Zealand was fixed and stored in 70% ethanol. All other material was stored dry.

Shell Measurements

Figure 1 shows the shell morphology measurements. Shell length (L), anterior end length (A), height (H), width (W), and interumbonal distance (L1) were measured for shell pairs and each valve. The ratios of these parameters to shell length (A/L, H/L, W/L, L1/L, respectively) were determined. Anterior and posterior teeth in each valve were also counted. Shell measurements were made using a caliper and an ocular micrometer with an accuracy of 0.1 mm.

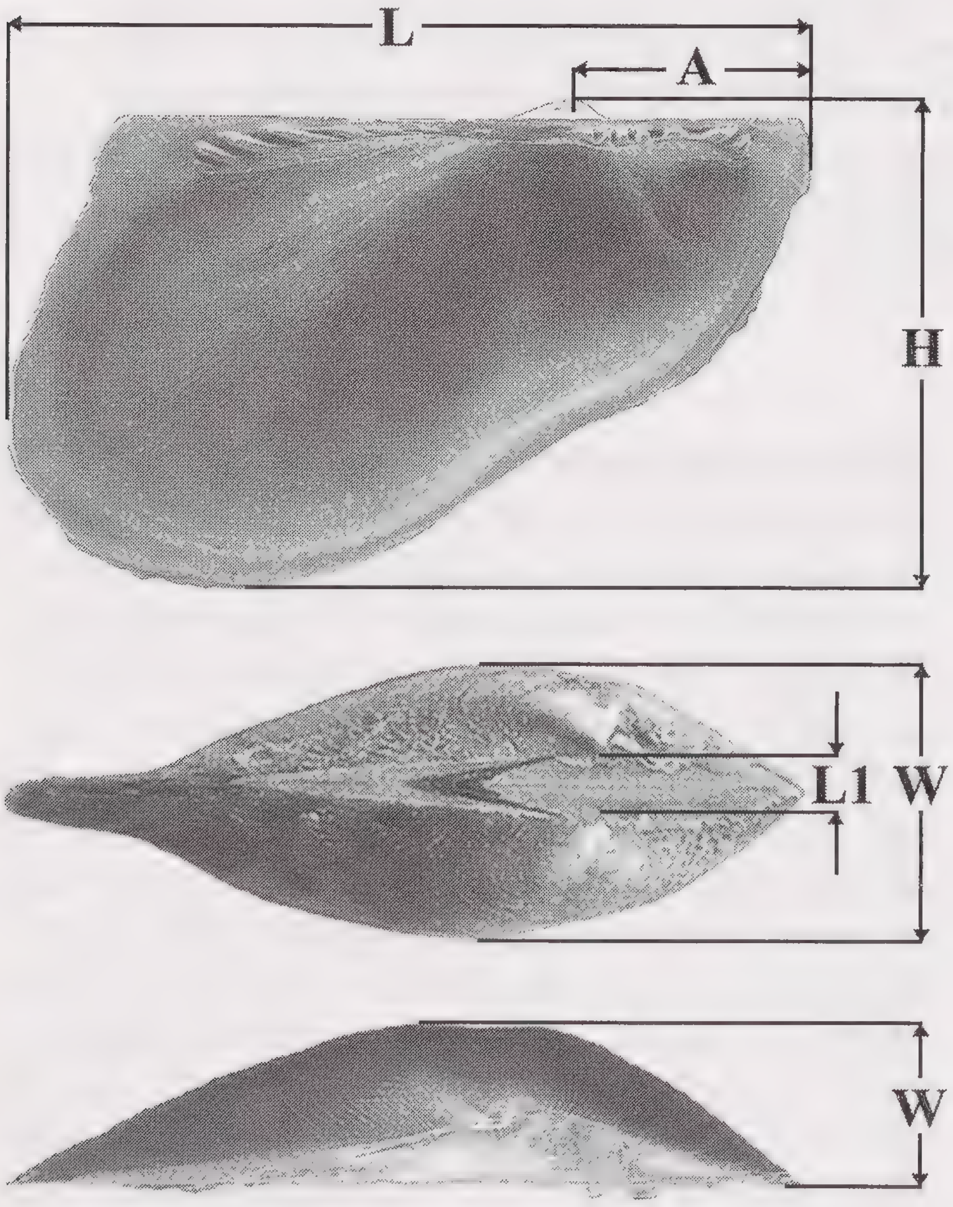


FIG. 1. Placement of shell measurements: L – length; H – height; A – anterior end length; W – width; L1 – interumbonal distance.

The following material was measured:

(1) twenty-four specimens and four left valves of *Bentharca asperula* from the Pacific and Atlantic oceans: North Pacific (NMW 1955.158.10248, 6 specimens); Tufts Abyssal Plain, North Pacific (LACM 1976-84.10, 1 specimen); Kermadec Ridge, South Pacific (NMNZ M.174251, 6 specimens); southwestern Africa, Atlantic (MIMB 12373 (donation from NMW), 10 specimens); Azores, North Atlantic (LACM 70-255.2, 1 specimen); Florida, North Atlantic (NMW 1955.158.10247, 4 left valves).

(2) ten specimens of *Asperarca nodulosa* from Norway, northeastern Atlantic (NMW 1955.158.10252, 6 specimens; NMW 1955.158.10253, 4 specimens).

(3) nine specimens of *Bentharca xenophoricola* from Japan, northwestern Pacific (NMW 1955.158.10256, 7 specimens; NMW 1955.158.10257, 2 specimens).

(4) six specimens of *Bentharca rubrotincta* from the Ryukyu Archipelago, Japan, northwestern Pacific (NSMT 51916).

Methods Used

For scanning electron microscopy, shells were cleaned of traces of soft tissues and periostracum in a strong commercial bleach, washed in distilled water, and dried. They were then mounted on aluminium stubs using adhesive tape and coated with gold for examination with a LEO 430.

Abbreviations

The following institutional abbreviations are used in the paper: AMS – Australian Museum, Sydney; CAS – California Academy of Sciences, San Francisco; IMB – Institute of Marine Biology, Russian Academy of Sciences, Vladivostok; LACM – Natural History Museum of Los Angeles County, Los Angeles; MIMB – Museum of the Institute of Marine Biology, Vladivostok; NMNZ – Museum of New Zealand Te Papa Tongarewa, Wellington; NMW – National Museums & Galleries of Wales, Cardiff; NSMT – National Science Museum, Tokyo; RBCM – Royal British Columbia Museum, Victoria; SAM – South African Museum, Cape

Town; SBMNH – Santa Barbara Museum of Natural History, Santa Barbara, California; UW – University of Washington, Seattle; ZIN – Zoological Institute, Russian Academy of Sciences, St. Petersburg.

SYSTEMATICS

Family Arcidae Lamarck, 1809
Genus *Asperarca* Sacco 1898

Type species

Arca nodulosa Müller, 1776, original designation by Sacco, 1898: 10.

Diagnosis

Shell small (< 15 mm), moderately thick to thick, moderately inflated, ovate-trapezoidal to subrectangular, equivalve or slightly inequivalve (left valve sometimes larger and more inflated), strongly inequilateral. Umbones strongly anterior, prosogyrate. Cardinal area wide. Shell surface with a byssal flexure more expressed in left valve. Sculpture of slightly imbricated commarginal lamellate ridges, made crenulate or nodulose by closely spaced, wide radial riblets. Periostracum thin, sometimes slightly hirsute, with short setae along posteroventral margin. Hinge plate narrow, slightly curved. Teeth divided into anterior and posterior sets by an edentulous gap; anterior teeth short, subvertical or oblique; posterior teeth longer, more oblique. Adductor scars slightly raised. Byssal sinus faint to moderate. Ligament external, opisthodetic.

Remarks

The genus *Asperarca* with the type species *A. nodulosa* was separated by Sacco (1898) when he studied *Acar* cf. *nodulosa* (Müller) and described its "varieties" *subandosa, perelliptica, carinatula*, and *subelliptica*. Subsequently, Newell (1969) synonymized it with *Barbatia* Gray, 1842, and until recently *A. nodulosa* was placed to *Bentharca* (Oliver & Allen, 1980; Oliver & Cosel, 1993). However, La Perna (1998) showed that *A. nodulosa*, together with a few Miocene species and two small Mediterranean species, form a distinct group to which the genus name *Asperarca* should be applied. Based on analysis of Noda's work (Noda, 1988), La Perna (1998) also noted that in shell morphology *B. xenophoricola* is similar to *Asperarca* rather than to *Bentharca*. Besides the morphological similarity, the bathymetric range of *B. xenophoricola* is in accord with the ecological range of *Asperarca* (La Perna, 1998).

After examination of the shell morphology of *B. xenophoricola* and type species of the genera *Asperarca* and *Bentharca* – *A. nodulosa* and *B. asperula*, respectively (Figs. 2–42, Tables 1–5), it is clear that *B. xenophoricola* should be recognized as a species of *Asperarca*. *Bentharca xenophoricola* (Figs. 30–42, Tables 4–5) differs from *B. asperula* (Figs. 2–16, Tables 1–2) in having the more angular, elongate, inflated and thicker shell, a less expanded posterior shell end, posterior radial carina, stronger radial sculpture, weakly developed hirsute periostracum, narrow edentulous gap between the anterior and posterior sets of teeth. In shell morphology, *B. xenophoricola* is more similar to *A. nodulosa* (Figs. 17–29, Tables 1, 3), with which it shares the angular, elongate, inflated and thick shell, a less expanded posterior shell end, well-defined radial carina, strong radial sculpture, weakly developed hirsute periostracum, and a relatively narrow edentulous gap. Therefore, following the recommendation of La Perna (1998), *B. xenophoricola* is here assigned to *Asperarca*.

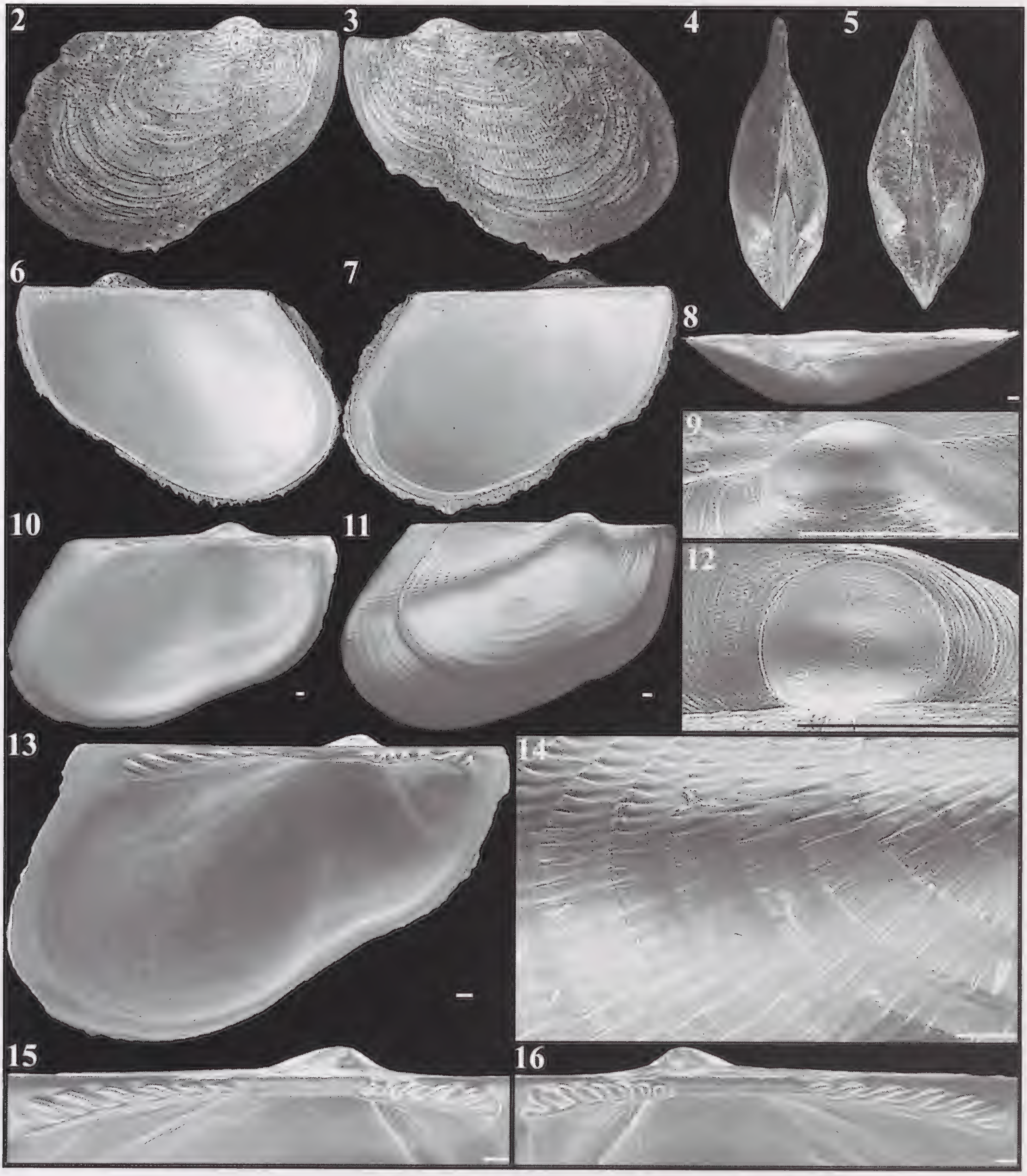
In addition to *B. xenophoricola*, four small species of *Bentharca* (shell length up to 4.0 mm) were recorded from off Japan. These are *Bentharca tenuis* Hayami & Kase, 1993; *Bentharca decorata* Hayami & Kase, 1993; *Bentharca irregularis* Hayami & Kase, 1993; and *Bentharca excavata* Hayami & Kase, 1993, described from the sublittoral caves of Ryukyu Islands (Hayami & Kase, 1993; Okutani, 2000). In shell morphology, these species are by far more similar to *Asperarca* than to *Bentharca*. The genus *Asperarca* now contains two small species (with a shell length up to 3.9 mm) described by La Perna (1998) from the Mediterranean Sea. Therefore, it is quite possible that following their detailed examination, four small species from coastal waters of Japan will also be placed in the genus *Asperarca*.

Asperarca xenophoricola (Kuroda, 1929)
(Figs. 30–42, Tables 4–5)

Bathyarca (?) *xenophoricola* Kuroda, 1929: 16, figs. 38–39.
Bathyarca (?) *xenophoricola* Kuroda – Kuroda, 1930: 33.

TABLE 1. Main morphological characters of the compared species. L – shell length; H – height; W – width; L1 – interumbonal distance.

Characters	*Bentharca asperula*	*Asperarca nodulosa*	*Asperarca xenophoricola*	*Deltaodon tugelae*	*Deltaodon rubrotincta*
Shall shape (H/L)	Trapezoidal, with strongly expanded posterior end; high (0.679)	Trapezoidal, elongate, with expanded posterior end; moderately high (0.613)	Trapezoidal, elongate, with expanded posterior end; moderately high (0.604)	Trapezoidal, with expanded posterior end; very high (0.764)	Trapezoidal, with strongly expanded posterior end, reddish brown with white rays and spots; high (0.667)
Valve (W/L)	Moderately inflated (0.379)	Very inflated (0.468)	Very inflated (0.444)	Moderately inflated (0.412)	Moderately inflated (0.373)
Interumbonal distance (L1/L)	Large (0.111)	Small (0.062)	Large (0.103)	Very small	Very small (0.023)
Sculpture	Wide, low commarginal ridges and wide, flat, closely spaced radial riblets	Wide, slightly imbricated, commarginal lamellate ridges and wide, high, closely spaced radial riblets	Wide, slightly imbricated, commarginal lamellate ridges, made nodulose by wide, high, closely spaced radial riblets	Wide, slightly imbricated, commarginal lamellate ridges and widely spaced radial riblets in middle part of shell	Wide, slightly imbricated, commarginal lamellate ridges and nodulose, widely spaced radial riblets of varying breadth
Periostracum	Thick, gray or brown, strongly hirsute; dense setae broad to narrow	Thin, pale gray, weakly hirsute, with thin, short setae	Thin, pale gray or pale brown, weakly hirsute, with thin, short setae	Thin, hairless	Thin, pale gray, weakly hirsute, with thin, short setae
Byssal flexure	Shallow	Very shallow	Deep	Absent in adult specimens	Shallow
Hinge plate	Subhorizontal, narrow	Slightly curved, narrow	Slightly curved, narrow	Curved, broad, strongly widening anteriorly and posteriorly	Curved, broad, strongly widening anteriorly and posteriorly
Edentulous gap	Wide, smooth	Narrow, smooth	Narrow, smooth	Very narrow, with shallow oblique groove	Very narrow, with shallow oblique groove
Hinge (number of teeth)	Anterior teeth short, subvertical (4–10); posterior teeth longer, oblique (4–8)	Anterior teeth short, oblique (4–6); posterior teeth longer, oblique (10–12)	Anterior teeth subvertical (7–14); posterior teeth oblique (6–9)	Anterior teeth long, curved, some bifid at their lower ends (8–9); posterior teeth long, oblique to subhorizontal (9–13)	Anterior teeth long, oblique, mostly curved, boomerang-shaped (4–7); posterior teeth long, oblique (9–18)



FIGS. 2–16. *Bentharca asperula.* FIGS. 2–3, 6–7: Exterior and interior views of right (length 10.1 mm) and left (length 10.3 mm) valves, southwestern Africa, 3975 m (MIMB 12373); FIG. 4: Dorsal view of both valves (shell length 8.8 mm), North Pacific (35°49'N, 179°57'W), 4605 m (NMW 1955.158.10248); FIG. 5: Dorsal view of both valves (shell length 8.9 mm), Kermadec Ridge (31°06.39'S, 179°02.05'W), New Zealand, 1522 m (NMNZ M. 174251); FIG. 8: Dorsal view of the left valve (MIMB 12373); FIGS. 9, 12: Prodissoconch of left valve (MIMB 12373); FIG. 10: Interior view of left valve without periostracum (MIMB 12373); FIGS. 11, 14: Exterior view and sculpture of right valve without periostracum (MIMB 12373); FIG. 13: Interior view of left valve (NMNZ M. 174251); FIGS. 15–16: Hinge of left and right valves (MIMB 12373). Scale bars = 300 µm.

Arca (*Bathyarca*) *xenophoricola* (Kuroda), 1929 – Nomura & Zinbo, 1934: 114.
Bentharca xenophoricola (Kuroda) – Habe, 1951: 33, figs. 45–46.

Type Locality

Kij Peninsula (central Honshu), 241 m (Kuroda, 1930; Higo et al., 1999).

Material Examined

Nine specimens from Kij, Japan, Northwest Pacific (NMW 1955.158.10256, 7 specimens; NMW 1955.158.10257, 2 specimens); 1 right and 1 left valves (AMS C 047185 together with *S. strabo*), 22 mi E of Narrabeen, N of Sydney, New South Wales, Australia (33°42'S, 151°43'E), 146 m, Coll. W. A. Haswell, 7-VI-1906 (HMCS "Miner"); 5 right and 7 left valves (AMS C 019797 together with *S. strabo*), 12.5 mi E of Cape Byron, New South Wales, Australia (28°38'S, 153°52'E), 203 m, Coll. G. H. Halligan, 10-XI-1902.

Description

Exterior: Shell small (to 12.0 mm), trapezoidal, elongate [H/L = 0.598 ± 0.051 (0.533–0.656)], distinctly inequivalve (left valve slightly larger and more inflated), inflated [W/L = 0.444 ± 0.030 (0.406–0.490)], strongly inequilateral, thick, solid, white under periostracum, with a moderate byssal gape. Sculpture of slightly imbricated commarginal lamellate ridges, made nodulose by closely spaced, wide, high radial riblets. Periostracum thin, pale gray or pale brown, weakly hirsute, with short, thin setae along posteroventral shell margin. Umbones small, low, rounded, well anterior to midline [A/L = 0.329 ± 0.034 (0.290–0.373)]. Interumbonal distance large [L1/L = 0.103 ± 0.014 (0.095–0.130)]. Cardinal area lanceolate, flat, wide, widest in front of umbones, anteriorly and posteriorly demarcated by ridges. Anterior shell end reduced, pointed. Posterior end expanded, drawn out, sharply rounded, slightly flexed to right, with a faint radial carina from beaks to ventral limit of posterior end. Central part of valves with a distinct, deep byssal flexure (more expressed in left valve) from beaks to ventral byssal gape. Anterodorsal margin straight, forming a sharp angle at transition to anterior margin. Anterior margin slightly convex, directed posteriorly, smoothly transitioning to ventral margin. Posterodorsal margin straight, forming a distinct obtuse angle at transition to posterior margin. Posterior margin concave, directed posteriorly, forming a rounded angle at transition to ventral margin. Ventral margin deeply concave in area of byssal gape (concavity more conspicuous in left valve). Ligament opisthodetic, wide, short. Prodissoconch small (length 200–220 μm), D-shaped, smooth.

TABLE 2. *Bentharca asperula*. Summary statistics of shell measurements (mm) and indices for separated valves and whole shells: L – valve length; H – height; W – width; A – anterior end length; L1 – interumbonal distance. Numerator indicates the summary statistics for the right valve, denominator – for the left valve.

	Separated valves							Whole shells					Number of teeth	
Statistics	L	H	W	L	H/L	W/L	A/L	L1	H/L	W/L	A/L	L1/L	Anterior	Posterior
Mean	9.19	6.07	1.98	2.82	0.661	0.215	0.306							
	8.56	5.76	2.03	2.59	0.679	0.241	0.302	0.96	0.666	0.379	0.282	0.111	-	-
SE	0.36	0.25	0.11	0.13	0.011	0.008	0.007							
	0.43	0.25	0.10	0.14	0.013	0.009	0.006	0.06	0.006	0.007	0.009	0.006	-	-
SD	1.29	0.91	0.39	0.45	0.041	0.029	0.025							
	1.76	1.02	0.40	0.59	0.052	0.037	0.024	0.29	0.019	0.025	0.028	0.021	-	-
Min	5.7	3.9	1.2	1.7	0.581	0.172	0.252						4	4
	5.9	4.0	1.4	1.7	0.588	0.178	0.252	0.2	0.643	0.348	0.245	0.072	4	4
Max	10.9	7.3	2.6	3.6	0.726	0.274	0.333						10	8
	11.2	7.3	2.7	3.6	0.800	0.308	0.333	1.5	0.693	0.424	0.326	0.158	10	8
N	13	13	13	13	13	13	13						13	13
	17	17	17	17	17	17	17	23	11	11	11	23	17	17

Interior: Hinge plate slightly curved, narrow. Teeth divided into anterior and posterior sets by a narrow edentulous gap posterior to beaks. Anterior set long, with 7–14 teeth: posteriormost teeth very small, subvertical; anteriormost teeth large, more oblique. Posterior set with 6–9 oblique teeth diverging in varying degree: anteriormost teeth small, lamellate, subhorizontal; posteriormost teeth large, oblique. Adductor scars rounded-triangular, slightly raised, unequal; posterior adductor scar larger than anterior. Shell interior white, with weak radial lines more conspicuous near pallial line.

Variability

Shell shape and proportions vary slightly (Tables 4–5). The shape of the posterior shell end varies from fairly rounded to elongate, angular-rounded. Some specimens have a straight instead of concave posterior shell margin. Relative height and convexity of the shell and the position of beaks are also slightly variable. Teeth of the anterior set vary a great deal in shape. In two specimens, the teeth are conically shaped and irregularly arranged. In another specimen, almost all anterior teeth are curved and expanded dorsally. Anterior and posterior teeth diverge to a markedly variable degree. The canting angle of the anterior teeth varies from 45° to 85°. The canting angle of the posterior tooth set is 10° to 45° for the anteriormost teeth and 30° to 60° for the posteriormost teeth.

Distribution and Habitat

Asperarca xenophoricola occurs off Japan from Suruga Bay, Honshu to Kyushu (Kuroda, 1930; Habe, 1958, 1977, 1981; Habe et al., 1986; Higo et al., 1999; Okutani, 2000), in the South China Sea (Higo et al., 1999), off China (Li, 1984), and off southeastern Australia [33°42'S, 151°43'E, 146 m (AMS C 433165); 28°38'S, 153°52'E, 203 m (AMS C 019797)]. This species has been recorded at depths from 50 m to 500 m, on rubble, attached to shells of gastropods *Xenophora japonica* (Kuroda & Habe, 1971) and *Xenophora pallidula* (Reeve, 1842) (Higo et al., 1999; Okutani, 2000).

Comparisons

This species is easily distinguished from other species of the genus by its less keeled, strongly inequivalve shell with sharply rounded posterior end, deep byssal flexure, and deeply concave posterior and ventral margins. It further differs in that the anterior tooth set is long, with a larger number of teeth and the posterior set consists of small, lamellate, subhorizontal teeth as well as large, oblique teeth.

TABLE 3. *Asperarca nodulosa*. Summary statistics of shell measurements (mm) and indices for separated valves and whole shells: L – valve length; H – height; W – width; A – anterior end length; L1 – interumbonal distance. Numerator indicates the summary statistics for the right valve, denominator – for the left valve.

	Separated valves							Whole shells					Number of teeth	
Statistics	L	H	W	A	H/L	W/L	A/L	L1	H/L	W/L	A/L	L1/L	Anterior	Posterior
Mean	8.72	5.32	2.24	2.62	0.613	0.256	0.300							
	8.90	5.34	2.20	2.62	0.602	0.246	0.294	0.52	0.571	0.468	0.287	0.062	-	-
SE	0.52	0.28	0.21	0.18	0.018	0.011	0.009							
	0.50	0.26	0.17	0.18	0.017	0.007	0.009	0.09	0.014	0.032	0.006	0.013	-	-
SD	1.17	0.62	0.46	0.40	0.040	0.024	0.020							
	1.12	0.59	0.32	0.40	0.037	0.015	0.020	0.29	0.031	0.072	0.013	0.028	-	-
Min	7.0	4.7	1.8	2.1	0.568	0.239	0.277						4	10
	7.3	4.7	1.8	2.1	0.547	0.235	0.274	0.2	0.547	0.393	0.268	0.034	4	10
Max	10.1	6.3	3.0	3.1	0.671	0.297	0.330						6	12
	10.3	6.3	2.8	2.8	0.644	0.272	0.326	1.1	0.625	0.556	0.299	0.107	6	12
N	5	5	5	5	5	5	5						5	5
	5	5	5	5	5	5	5	10	5	5	5	10	5	5

TABLE 4. *Asperarca xenophoricola.* Shell measurements (mm), indices and summary statistics of all characters for separated valves: L – valve length; H – height; W – width; A – anterior end length; L1 – interumbonal distance. Numerator indicates shell measurements and indices for the right valve, denominator – for the left valve.

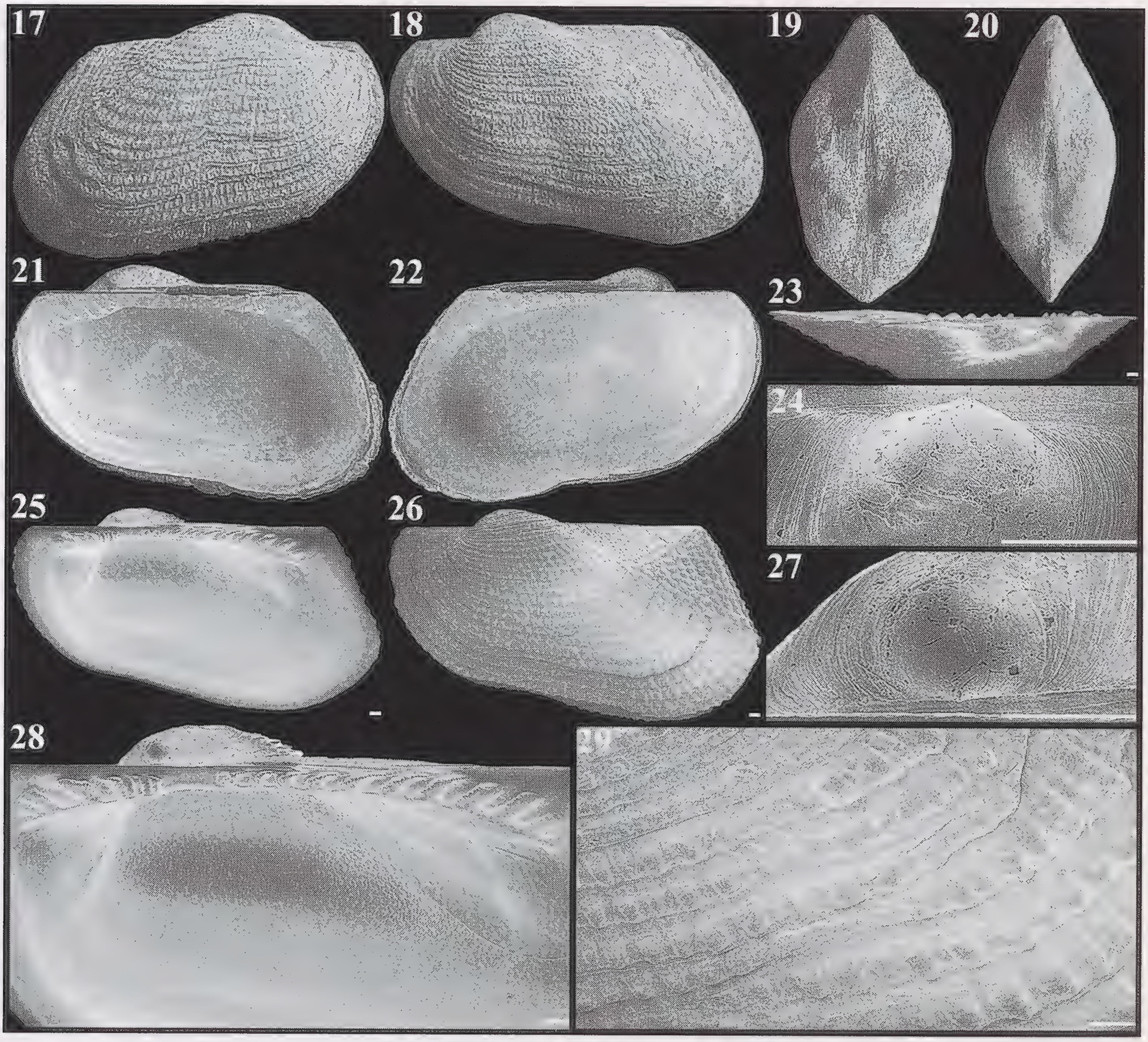
Specimen	L	H	W	A	H/L	W/L	A/L	Number of teeth	
								Anterior	Posterior
NMW	9.0	5.3	2.2	3.0	0.589	0.244	0.333	7	7
1955.158.10257	9.6	5.7	2.5	3.1	0.594	0.260	0.323	8	8
NMW	10.9	5.8	2.3	3.5	0.532	0.211	0.321	14	9
1955.158.10256	12.0	6.4	3.1	3.9	0.533	0.258	0.325	14	9
NMW	10.0	6.0	2.6	2.9	0.600	0.260	0.290	11	8
1955.158.10256	11.0	6.7	3.3	3.3	0.609	0.300	0.300	12	8
NMW	5.9	3.7	1.4	2.2	0.627	0.237	0.373	7	7
1955.158.10256	6.1	4.0	1.6	2.2	0.656	0.262	0.361	7	6

Statistics	L	H	W	A	H/L	W/L	A/L	Number of teeth	
								Anterior	Posterior
Mean	8.95	5.20	2.13	2.90	0.587	0.238	0.329		
	9.68	5.70	2.63	3.13	0.598	0.270	0.327	-	-
SE	1.09	0.52	0.26	0.27	0.020	0.010	0.017		
	1.29	0.60	0.38	0.35	0.025	0.010	0.013	-	-
SD	2.18	1.04	0.51	0.54	0.040	0.020	0.034		
	2.58	1.21	0.76	0.70	0.051	0.020	0.025	-	-
Min	5.9	3.7	1.4	2.2	0.532	0.211	0.290	7	7
	6.1	4.0	1.6	2.2	0.533	0.258	0.300	7	6
Max	10.9	6.0	2.6	3.5	0.627	0.260	0.373	14	9
	12.0	6.7	3.3	3.9	0.656	0.300	0.361	14	9
N	4	4	4	4	4	4	4	4	4
	4	4	4	4	4	4	4	4	4

TABLE 5. *Asperarca xenophoricola.* Shell measurements (mm), indices and summary statistics of all characters for whole shells: L – shell length; H – height; W – width; A – anterior end length; L1 – interumbonal distance.

Specimen	L	H	W	A	L1	H/L	W/L	A/L	L1/L
NMW 1955.158.10257	10.0	5.5	4.9	3.2	1.3	0.550	0.490	0.320	0.130
NMW 1955.158.10257	9.6	5.7	3.9	3.2	1.0	0.594	0.406	0.333	0.104
NMW 1955.158.10256	9.5	5.5	4.0	3.1	0.9	0.579	0.421	0.326	0.095
NMW 1955.158.10256	9.3	5.5	4.3	2.8	0.9	0.591	0.462	0.301	0.097
NMW 1955.158.10256	8.2	5.2	3.6	2.7	0.8	0.634	0.439	0.329	0.098
NMW 1955.158.10256	7.4	5.0	3.3	2.7	0.7	0.676	0.446	0.365	0.095

Statistics	L	H	W	A	L1	H/L	W/L	A/L	L1/L
Mean	9.00	5.40	4.00	2.95	0.93	0.604	0.444	0.329	0.103
SE	0.40	0.10	0.23	0.10	0.08	0.018	0.012	0.009	0.006
SD	0.99	0.25	0.56	0.24	0.21	0.044	0.030	0.021	0.014
Min	7.4	5.0	3.3	2.7	0.7	0.550	0.406	0.301	0.095
Max	10.0	5.7	4.9	3.2	1.3	0.676	0.490	0.365	0.130
N	6	6	6	6	6	6	6	6	6



FIGS. 17–29. *Asperarca nodulosa.* FIGS. 17–18, 21–22: Exterior and interior views of right (length 10.1 mm) and left (length 10.3 mm) valves, Norway, northeastern Atlantic (NMW 1955.158.10253); FIG. 19: Dorsal view of both valves (shell length 11.7 mm), Bergen, Norway, northeastern Atlantic (NMW 1955.158.10252); FIG. 20: Dorsal view of both valves (shell length 9.5 mm (NMW 1955.158.10253); FIGS. 23–25, 27–28: Dorsal and interior views, prodissoconch, and hinge of right valve (NMW 1955.158.10253); FIGS. 26, 29: Exterior view and sculpture of left valve without periostracum (NMW 1955.158.10253). Scale bars = 300 µm.

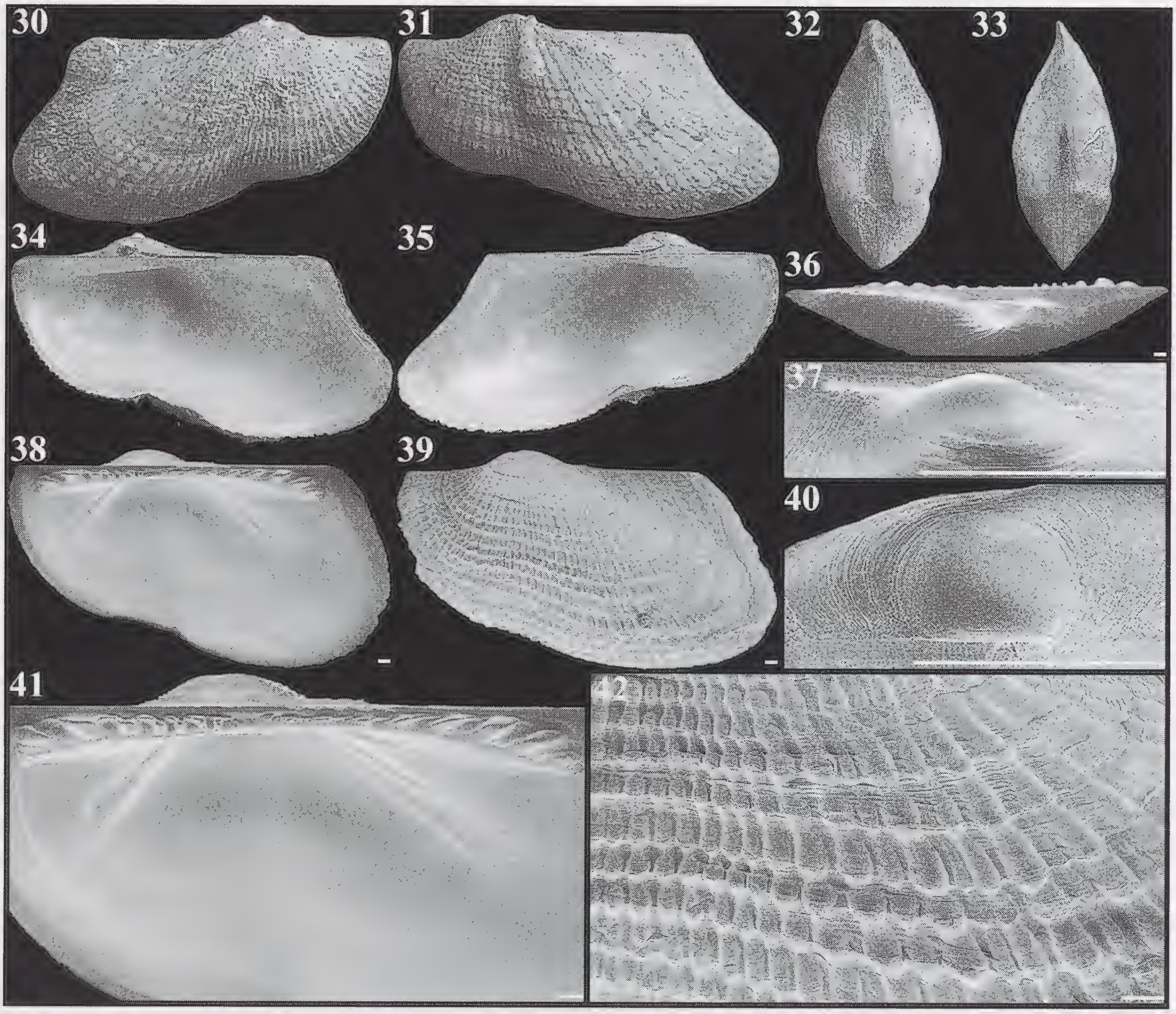
Genus *Deltaodon* Barnard, 1962

Type species

Deltaodon tugelae Barnard, 1962, by original designation.

Diagnosis

Shell small (< 26 mm), thick, moderately inflated, ovate-trapezoidal to trapezoidal, equivalve or slightly inequivalve (left valve sometimes larger and more inflated), strongly inequilateral. Umbones strongly anterior, prosogyrate. Cardinal area very narrow. Sculpture of lamellate commarginal ridges and nodulose, widely spaced radial riblets. Periostracum thin, sometimes slightly hirsute, with short setae along posteroventral margin. Hinge plate broad, curved, most concave and thin posterior to beaks. Teeth divided into anterior and posterior sets by a shallow oblique groove; anterior teeth long, angular, forming an oval group; posterior teeth oblique to subhorizontal. Adductor scars slightly raised. Byssal sinus faint or absent. Ligament external, opisthodetic.



FIGS. 30–42. *Asperarca xenophoricola.* FIGS. 30–31, 34–35: Exterior and interior views of right (length 10.9 mm) and left (length 12.0 mm) valves. Kiji, Japan, northwestern Pacific (NMW 1955.158.10256); FIG. 32: Dorsal view of both valves (shell length 10.0 mm), Kiji, Japan, northwestern Pacific (NMW 1955.158.10257); FIG. 33: Dorsal view of both valves (shell length 9.6 mm (NMW 1955.158.10257); FIGS. 36, 38, 41: Dorsal and interior views and hinge of right valve (NMW 1955.158.10257); FIGS. 37, 40: Prodissoconch of right valve (NMW 1955.158.10257); FIGS. 39, 42: Exterior view and sculpture of left valve without periostracum (NMW 1955.158.10257). Scale bars = 300 µm.

Remarks

This genus was omitted by Newell (1969) and is currently represented by a single species *D. tugelae*. Kilburn (1983) considered *Deltaodon* to be a subgenus of *Samacar* Iredale, 1936, because the posterior teeth of the type species, *D. tugelae*, are subparallel to the dorsal shell margin, as in the holotype of *S. strabo* (Hedley, 1915). However, the present study of type and extensive additional material of *S. strabo* showed that *Deltaodon* is unlike *Samacar* in having a very high shell with a non-hirsute periostracum, and a very broad, strongly curved hinge plate. It further differs in that the hinge teeth are separated into anterior and posterior sets by a very narrow, oblique groove, and very long, angular anterior teeth, sometimes bifid at their lower ends (Barnard, 1962; Kilburn, 1983; Kamenev, 2007). Taking into account the marked differences in shell and hinge morphology, *Deltaodon* is considered as a distinct genus (Kamenev, in press).

Examination of the shell morphologies of *B. rubrotincta* and the type species of the genus *Bentharca* has shown that *B. rubrotincta* differs from *B. asperula* (Figs. 2–16, 43–56, Tables 1–2, 7). The distinctive features of *B.*

TABLE 6. *Dealtaodon tugelae.* Shell measurements (mm), indices and summary statistics of all characters for separated valves: L – valve length; H – height; W – width (after Barnard, 1962).

Specimen	L	H	W	H/L	W/L
SAM Reg. No. A9477	9.0	7.0	2.0	0.778	0.222
SAM Reg. No. A9477	20.0	16.0	4.0	0.800	0.200
SAM Reg. No. A9477	20.0	14.5	3.5	0.725	0.175
SAM Reg. No. A9477	22.0	17.0	5.5	0.773	0.250
SAM Reg. No. A9477	25.0	19.0	5.0	0.760	0.200
Statistics	**L**	**H**	**W**	**H/L**	**W/L**
Mean	19.2	14.7	4.0	0.764	0.206
SE	2.71	2.06	0.61	0.016	0.016
SD	6.06	4.60	1.37	0.031	0.031
Min	9.0	7.0	2.0	0.725	0.175
Max	25.0	19.0	5.5	0.800	0.250
N	5	5	5	5	5

rubrotincta are a thicker shell, with a very narrow cardinal area; stronger radial sculpture; weakly developed hirsute periostracum; broad, strongly curved hinge plate; the presence of oblique groove between the anterior and posterior tooth sets; large, curved anterior teeth; and a very long posterior tooth set with a larger number of teeth. In shell morphology and hinge structure, *B. rubrotincta* is most similar to the type species *Deltaodon* (Figs. 57–61, Table 6). Both have a thick shell, with a very narrow cardinal area, broad and strongly curved hinge plate, with an oblique groove separating the anterior and posterior tooth sets, and large, curved anterior teeth forming an oval group (Tables 1, 6–7). Therefore, *B. rubrotincta* is referred to *Deltaodon.*

Deltaodon rubrotincta (Kuroda & Habe in Habe, 1958)
(Figs. 43–56; Table 7)

Bentharca rubrotincta Kuroda & Habe in Habe, 1958: 252–253.
Bentharca rubrotincta Kuroda & Habe, 1958 – Habe, 1977: 34; Li, 1984: 157, pl. 2, fig. 10.
Bentharca xenophoricola (Kuroda) – Noda, 1988: pl. 1, figs. 13a–15b.
Porterius pacificus (Nomura & Zinbo) – Noda, 1988: pl. 1, fig. 5a–b.

Type Locality

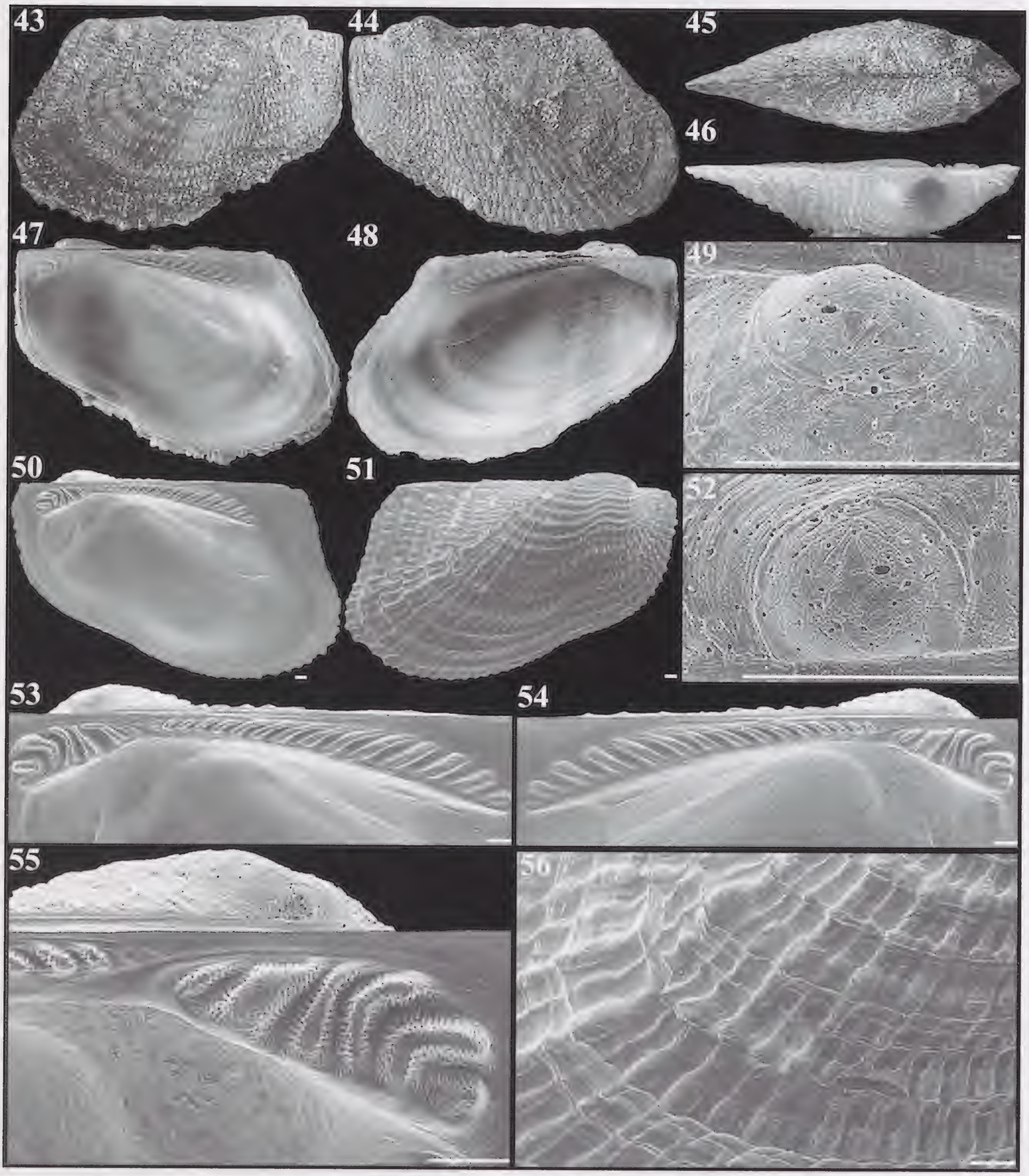
Bungo Strait off western Shikoku, between Kyushu and Shikoku, 110 m, gravel and shells (Habe, 1958; Higo et al., 1999).

Material Examined

Six specimens from Miyako-Jima Islands, Ryuku Archipelago, Japan, 150 m (NSMT 51916).

Description (expanded from Habe, 1958)

Exterior: Shell small (to 12.6 mm), trapezoidal, high [H/L right valve = 0.653 ± 0.024 (0.610–0.691); H/L left valve = 0.667 ± 0.026 (0.632–0.703)], slightly inequivalve (left valve slightly larger and more inflated), moderately inflated [W/L right valve = 0.212 ± 0.013 (0.193–0.232); W/L left valve = 0.230 ± 0.017 (0.206–0.257)], strongly inequilateral, thick, solid, reddish-brown, with white rays and spots. Sculpture of slightly imbricated, wide, commarginal lamellate ridges and high, nodulose, widely spaced radial ribs of varying breadth. Periostracum thin, pale gray, weakly hirsute, with short, thin setae along posteroventral shell margin. Umbones small, low, rounded, prosogyrate, strongly anterior to midline [A/L right valve = 0.201 ± 0.039 (0.158–0.258); A/L left valve = 0.192 ± 0.035 (0.143–0.242)]. Interumbonal distance very small [L1/L = 0.023 (0.015–0.032)]. Cardinal area needle-shaped in dorsal view, very narrow, widest in front of umbones, span roof-shaped in cross section, anteriorly delineated by termination of sculpture, and posteriorly demarcated by ridges. Anterior shell end reduced, slightly angular. Posterior end expanded, angular rounded, slightly flexed to right, with a faint radial carina from beaks to ventral limit of posterior end. Central part of valves with a distinct byssal flexure (more expressed in left valve), extending from beaks to ventral byssal gape. Anterodorsal margin straight, forming a sharp angle at transition to anterior margin. Anterior margin almost straight, slightly directed posteriorly, smoothly transitioning to ventral margin. Posterodorsal margin straight, forming a distinct obtuse angle at transition to posterior margin. Posterior margin slightly concave, posteriorly directed, forming a rounded angle at transition to ventral



FIGS. 43–56. *Deltaodon rubrotincta.* Miyako-Jima Islands, Ryukyu Archipelago, 150 m (NSMT 51916). FIGS. 43–45, 47–48: Exterior and interior views of right (length 10.9 mm) and left (length 12.0 mm) valves, and dorsal views of both valves; FIGS. 46, 49–50, 52–53: Dorsal and interior views, prodissoconch, and hinge of right valve; FIGS. 51, 56: Exterior view and sculpture of right valve without periostracum; FIGS. 54–55: Hinge of left valve. Scale bars = 300 μm.

margin. Ventral margin slightly concave in area of byssal gape (concavity more conspicuous in left valve). Ligament opisthodetic, narrow, long (more than ½ of posterior part of cardinal area). Prodissoconch small (length 205–215 µm), D-shaped, smooth.

Interior: Hinge plate broad, strongly curved, most concave and thinnest posterior to beaks, strongly widening anteriorly and posteriorly, with a conspicuous ligamental groove under posterior teeth. Teeth divided into anterior and posterior sets by a shallow, oblique groove posterior to beak. Anterior set short, forming an oval group of 4–7 teeth; posterior set long, with 9–18 teeth. Anterior teeth long, large, oblique, mostly curved, boomerang-shaped. Posterior teeth long, increasing in size, oblique, diverging to a varying degree, inner teeth slightly curved. Adductor scars rounded-triangular, slightly raised, unequal; posterior adductor scar larger than anterior. Shell interior reddish-brown, with white rays and spots, and with weak radial lines more conspicuous near pallial line.

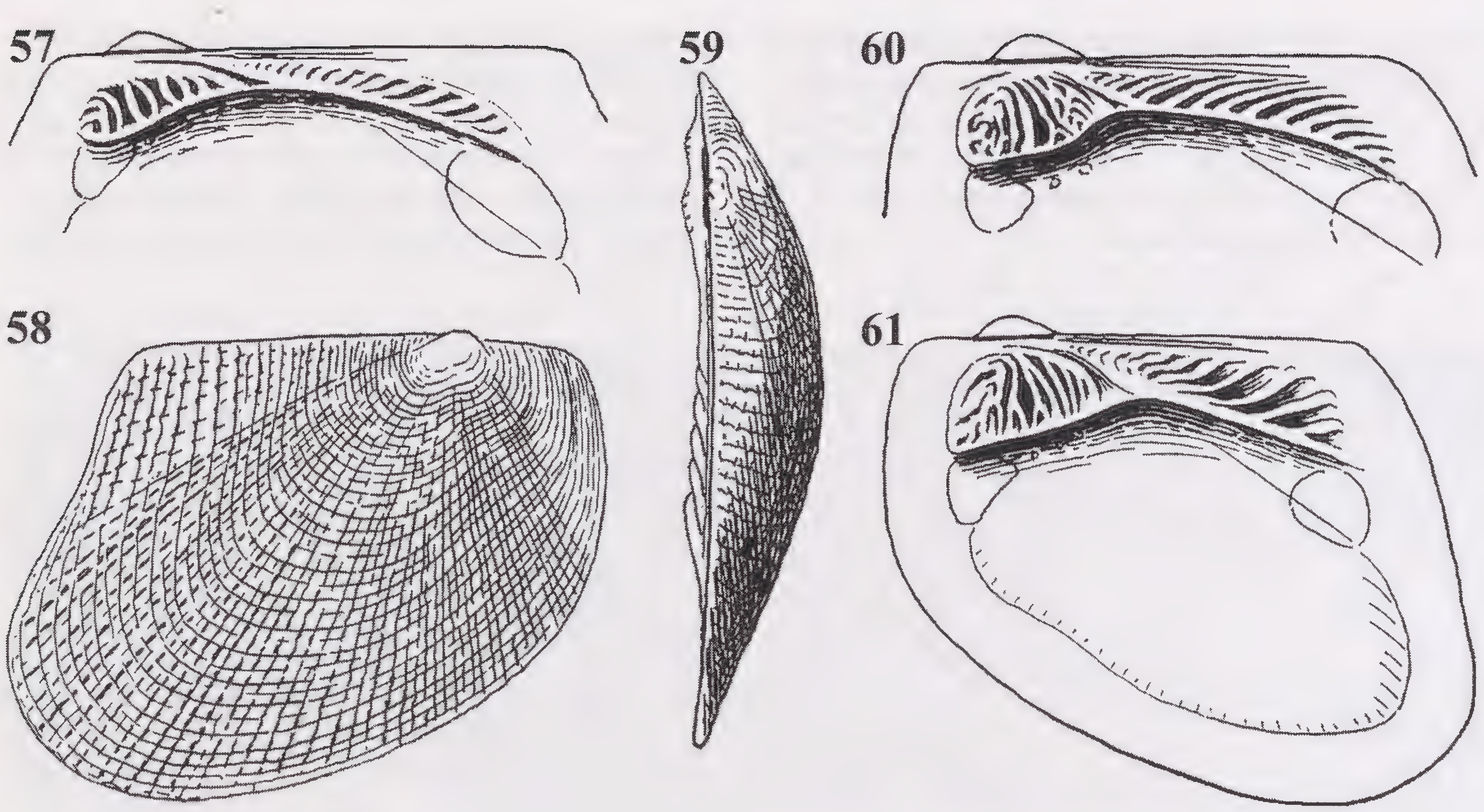
Variability

Shell shape and proportions vary little (Table 7). Relative height and convexity of the shell and the location of the beaks are slightly variable. The number of teeth in the anterior and

TABLE 7. *Deltaodon rubrotincta.* Shell measurements (mm), indices and summary statistics of all characters for separated valves: L – valve length; H – height; W – width; A – anterior end length; L1 – interumbonal distance. Numerator indicates shell measurements and indices for the right valve, denominator – for the left valve. NM – not measured.

Specimen	L	H	W	A	L1	H/L	W/L	A/L	L1/L	Number of teeth	
										Anterior	Posterior
Holotype (after Habe, 1958)	8.2	5.0	1.9	NM		0.610	0.232	NM		NM	NM
	9.5	6.0	2.2	NM	NM	0.632	0.232	NM	NM	NM	NM
NSMT 51916	11.4	7.5	2.2	1.8		0.658	0.193	0.158		7	18
	12.6	8.0	2.6	1.8	0.4	0.635	0.206	0.143	0.032	7	18
NSMT 51916	9.4	6.5	2.0	1.9		0.691	0.213	0.202		5	14
	10.1	7.1	2.6	2.0	0.2	0.703	0.257	0.198	0.020	6	14
NSMT 51916	8.9	5.8	1.8	1.5		0.652	0.202	0.169		6	16
	9.6	6.4	2.1	1.7	0.2	0.667	0.219	0.177	0.021	6	16
NSMT 51916	8.2	5.4	1.7	1.5		0.659	0.207	0.183		4	12
	8.6	5.9	2.0	1.5	0.2	0.686	0.233	0.174	0.023	5	13
NSMT 51916	3.8	2.5	0.8	0.9		0.658	0.211	0.237		4	11
	4.1	2.8	0.9	0.9	0.1	0.683	0.220	0.220	0.024	4	11
NSMT 51916	3.1	2.0	0.7	0.8		0.645	0.226	0.258		4	9
	3.3	2.2	0.8	0.8	0.05	0.667	0.242	0.242	0.015	4	10

Statistics	L	H	W	A	L1	H/L	W/L	A/L	L1/L	Number of teeth	
										Anterior	Posterior
Mean	7.57	4.96	1.59	1.40		0.653	0.212	0.201			
	8.26	5.49	1.88	1.45	0.19	0.667	0.230	0.192	0.023	-	-
SE	1.14	0.76	0.22	0.19		0.009	0.005	0.016			
	1.27	0.82	0.28	0.20	0.05	0.010	0.006	0.014	0.002	-	-
SD	3.02	2.02	0.59	0.46		0.024	0.013	0.039			
	3.36	2.17	0.74	0.49	0.12	0.026	0.017	0.035	0.006	-	-
Min	3.1	2.0	0.7	0.8		0.610	0.193	0.158		4	9
	3.3	2.2	0.8	0.8	0.05	0.632	0.206	0.143	0.015	4	10
Max	11.4	7.5	2.2	1.9		0.691	0.232	0.258		7	18
	12.6	8.0	2.6	2.0	0.4	0.703	0.257	0.242	0.032	7	18
N	7	7	7	6	6	7	7	6	6	6	6
	7	7	7	6	6	7	7	6	6	6	6



FIGS. 57–61. *Deltaodon tugelae.* FIG. 57: Hinge teeth of right valve of juvenile (length 9.0 mm); FIG. 58: Exterior view of right valve (length 20.0 mm); FIG. 59: Dorsal view of right valve. FIGS. 60–61: Hinge teeth of right valves of two shells to show variation (after Barnard, 1962).

posterior sets depends on the size of the specimen. The posterior teeth diverge to a variable degree. The canting angle of posterior teeth varies from 30° to 60°.

Distribution and Habitat

Deltaodon rubrotincta occurs off Japan from the Kii Peninsula to the Yaeyama Islands (Habe, 1958, 1981; Higo et al., 1999), in the East China Sea and South China Sea (Higo et al., 1999), and off China (Li, 1984). This species was recorded at depths from 100 m to 200 m, attached to rocks and stones (Habe, 1958, 1977; Higo et al., 1999).

Comparison

In contrast to *D. tugelae*, *D. rudrotincta* has a more elongate, reddish-brown shell, a narrower hinge plate, and shorter anterior teeth unbifid at their lower ends (Tables 1, 6–7).

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